African Invertebrates Vol. 48 (1) Pages 77–86 Pietermaritzburg April, 2007

An enigmatic Palaeozoic stem-group: Paoliida, designation of new taxa from the Upper Carboniferous of the Czech Republic (Insecta: Paoliidae, Katerinkidae fam. n.)

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ABSTRACT

Two new representatives of stem group Paoliida are described and illustrated from the Upper Carboniferous of the Upper Silesian Coal Basin (Czech Republic), i.e. *Katerinka hilaris* gen. et sp. n. (Katerinkidae fam. n.) and a further fragmentary specimen with uncertain familial attribution (?Paoliidae). Rediscovery of the missing holotype specimen *Holasicia sustai* Kukalová, 1958 enabled detailed study and description of the monotypic genus *Mertovia* gen. n., type species *Mertovia sustai* (Kukalová, 1958), comb. n. (Paoliidae). The material was classified and compared with all possibly related taxa on the basis of the wing venation. Some uncertainties on the current state of knowledge of certain taxa with similar wing-venation pattern and their systematic attribution were considered. The fossil record of Paoliidae is briefly discussed and a check-list is provided.

KEY WORDS: Paoliida, Paoliidae, Katerinkidae, Palaeozoic, Upper Carboniferous, Namurian, Westphalian A (Langsettian), Upper Silesian Coal Basin, Czech Republic, new taxa.

INTRODUCTION

The order Paoliida Handlirsch, 1906 (= Protoptera Sharov, 1966) is small group of pterygote insects with eight described genera and ten species known from a relatively short period in the Upper Carboniferous (Namurian B to Westphalian A (= Langsettian)). Paoliids were probably restricted to the territory within the Laurasian continent according to their presence in deposits of North America (East USA) and Europe (Belgium, Czech Republic, England, Germany, The Netherlands, Wales) (see Fig. 1). The difficulties with definitive assessment of particular extinct higher taxa based on fragmentary fossils were shown by Hennig (1981: 148) who traced paoliids as an interesting example.

Systematic attribution of the family Paoliidae within the order Palaeodictyoptera was primary established by Handlirsch (1906) who proposed a close relationship with spillapterids. He placed Scudder's two species into this new family on the basis of the spread-out and copious branching of the cubital and anal veins along the inner margin of the wing (Handlirsch 1906). Before that Brongniart (1883: 160) had assigned *Paolia vetusta* Smith, 1871 to protolocustids and on the contrary Scudder (1885*a*, *b*) attributed *Paolia vetusta* Smith, 1871 and ?*Paolia gurlei* Scudder, 1885 to protophasmids. At a later stage, Kukalová (1958*a*) in her extensive work on new taxa from the Upper Silesian Coal Basin, integrated this family as a group of 'Protorthoptera' (Cacurgoidea). Sharov (in Rodendorf 1962) first considered Paoliidae within 'Paraplecoptera' and subsequently included them in 'Archaeoptera', as a basal stem group of Pterygota (Sharov 1966). Carpenter (1992) placed Paoliidae within the most primitive Protorthoptera together with Homoeodictyidae and Thoronysididae, since these families have reticulate venation (so-called 'archedictyon') as well as a concave MP in the forewing. Further re-

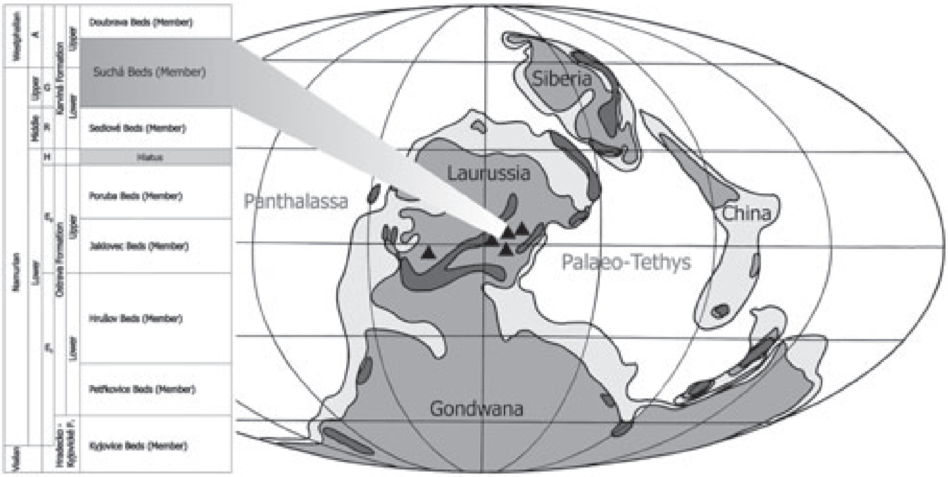

Westphalian
Namurian
Visean
Upper
Middle
Lower
A
G
R
H
E2
E1
Karviná Formation
Ostrava Formation
Hradecko-Kyjovické F.
Upper
Lower
Doubrava Beds (Member)
Suchá Beds (Member)
Sedlové Beds (Member)
Hiatus
Poruba Beds (Member)
Jaklovec Beds (Member)
Hrušov Beds (Member)
Petřkovice Beds (Member)
Kyjovice Beds (Member)
Siberia
Laurussia
Panthalassa
China
Palaeo-Tethys
Gondwana

Fig. 1. Location of the Upper Silesian Coal Basin (Czech Republic) within Upper Carboniferous palaeogeographical world map and stratigraphical position in lithostratigraphic division of the Carboniferous in the Upper Silesian Coal Basin the Czech Republic after Dopita *et al*. (1997, modified). Proximate distribution of other paoliid species within palaeogeographical world map indicated by black triangles (palaeogeographical map after Scotese (2005), modified).

arrangement into the 'hemipteroid lineage' was done by Kukalová-Peck and Brauckmann (1992) based on the presence of an 'arculus' between veins MP and CuA and simultaneously a simple CuP or only terminal twigging. Finally Rasnitsyn (Rasnitsyn 1976; Rasnitsyn & Quicke 2002, fig. 1) considered paoliids as a basal stem group of the Pterygote lineage as was proposed by Sharov (1966), but without any distinct synapomophies.

The Upper Silesian Basin (USB) is a triangular sedimentary structure situated partly in the NE of Moravia (Czech Republic) and mainly in the Silesian part of Poland (see Dopita *et al.* 1997: 34). From a palaeogeographical point of view, it is similar to the coal basins of the European Variscides from Wales through Belgium to northern Germany. These basins form part of the Subvariscicum. The USB was formed as a top molasse stage of the polytypic foreland basin (Dopita *et al.* 1997). The basin is filled with Lower and Upper Carboniferous continental and marine sediments divided into three main lithostratigraphical units (Hradecko-Kyjovické Formation, Ostrava Formation, Karviná Formation) in the Czech region (see Fig. 1). Zoopalaeontological and phytopalaeontological records were extensively reviewed by Řehoř and Řehořová (1972) and Dopita *et al.* (1997). Fossil insects were found almost entirely from the Karviná Formation (Suchá Beds Member) described by Kukalová (1958*a*, *b*, 1959, 1960, 1964). Recently, a single specimen attributed within Archaeorthoptera was discovered from the drilling core in the basal part of the Ostrava Formation (Petřkovice Beds Member) and published by Prokop *et al*. (2005).

MATERIAL AND METHODS

The material was kept in a dry state without further fixation and deposited in the palaeontological collection of the Municipal Museum in Ostrava (Czech Republic). Standard techniques of observation under a stereomicroscope (Olympus SZX 9/12) and digital photography (Olympus 5060, Nikon 4500) were employed to examine the material in the dry state or under ethyl alcohol. The classical preparation technique was applied.

We follow the wing-venation nomenclature of Kukalová-Peck and Brauckmann (1992).

TAXONOMY

Order Paoliida Handlirsch, 1906

Family Paoliidae Handlirsch, 1906

Type genus: *Paolia* Smith, 1871.

List of included genera, after Carpenter (1992) and Brauckmann (1984) and reviewed by Rasnitsyn (Rasnitsyn & Quicke 2002): *Holasicia* Kukalová, 1958; *Kemperala* Brauckmann, 1984; *Olinka* Kukalová, 1958; *Paolia* Smith, 1871; *Paoliola* Handlirsch, 1919; *Pseudofouquea* Handlirsch, 1906; *Sustaia* Kukalová, 1958; *Zdenekia* Kukalová, 1958 (see Appendix).

Genus **Mertovia** gen. n.

Etymology: Named after E. Mertová, curator of palaeontology in Municipal Museum in Ostrava; feminine gender.

Type species: *Holasicia sustai* Kukalová, 1958, by present designation.

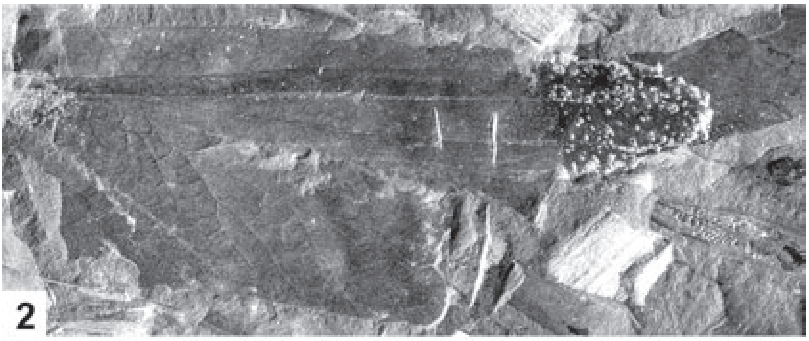
Diagnosis: Based on fore-wing venation, *Mertovia* gen. n. differs from all other paoliid genera by the following combination of characters: ScP ending on costal margin a little above wing apex; RA simple and straight, probably ending well before wing apex; RP parallel to RA and simple, without clear distal branches, probably reaching wing margin at wing apex (estimated from the fragment); MP with a neutral convexity, divided into two (maybe three) posterior branches in its distal half; a very strong convex 'arculus' between CuA and MP just opposite the fork of RA and RP; CuA convex, with 5 or 6 posterior branches ending in CuP or in posterior wing margin; simple CuP strongly concave; three convex anal veins.

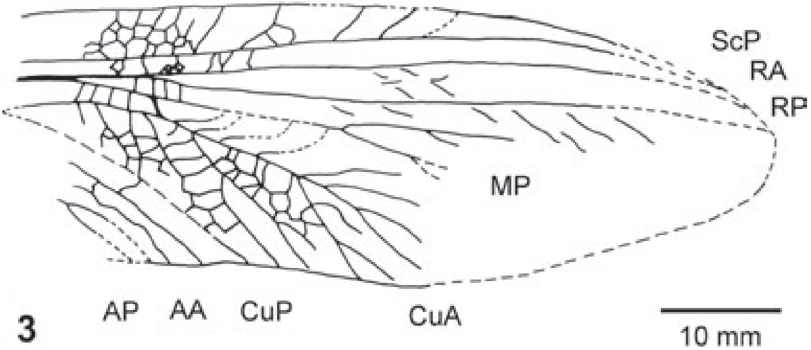
Mertovia sustai (Kukalová, 1958), **comb. n.**

Figs 2, 3

Protoblatoid sp. (Cacurgidae): Šusta 1928: 414, pl. 17, fig. 8.
Holasicia sustai: Kukalová 1958: 943, fig. 4.

Redescription: Distal two-thirds of fore wing with dark coloration, no spot or other colour pattern, with clearly visible reticulate venation (so-called 'archaedictyon') and rather thick membrane; fragment 52 mm long, probable complete length about 75 mm, maximum width 24 mm; area between C and ScP 4.4 mm wide, with net of small cells and veinlets in basal half and 4 or 5 weak branches of ScP in distal half; ScP clearly concave, ending on costal margin a little above wing apex; RA convex, straight and simple, with no branches, probably ending well before wing apex; RP diverging from R about 54.4 mm from wing apex, basally with neutral convexity and clearly concave in its distal half, with net of veinlets between it and RA and between it and M; RP simple, without clear distal branches, parallel to RA, probably reaching wing margin at wing apex; base of M poorly preserved, with convex MA between M and R not visible; MP





Figs 2, 3. *Mertovia sustai* (Kukalová, 1958), comb. n. (Paoliidae), photograph and line drawing of holotype specimen B13189, collection of the Municipal Museum of Ostrava.

with neutral convexity, divided into two (maybe three) posterior branches in its distal half; very strong convex 'arculus' between CuA and MP, about 53.5 mm from wing apex, opposite base of RP; CuA convex, with 5 or 6 posterior branches ending in CuP or in posterior wing margin; several oblique veinlets between CuA and MP and three anterior branches emerging from CuA distally, with apparent trichotomy between first anterior branch of CuA, main CuA and posterior branch of CuA; point of separation between CuA and CuP not preserved, but very basal; CuP strongly concave; three convex anal veins partly visible.

Holotype: specimen B13189, imprint of the distal two-thirds of well preserved fore wing (originally Šusta coll.). CZECH REPUBLIC: Upper Silesian Coal Basin, Hlubiná Pit in Karviná, hanging wall seam (No. 24); Upper Carboniferous, Westphalian A (Langsettian), Upper Suchá Beds (Member), Karviná Formation.

Discussion: The description of *H. sustai* was originally based only on a photograph of '*Protoblatoid* sp.' from Šusta's work (1928: 414, pl. XVII, fig. 8), because at that time it was impossible to locate the specimen within the collection. Nevertheless, Kukalová believed that one day it could be recovered in the collection of the Municipal Museum in Ostrava. Subsequently, the missing holotype specimen did reappear during the transfer of the collection to another site. This rediscovery enabled a detailed study of the wing venation (Figs 2, 3) and subsequent redescription.

The organisation of the median vein with a strong convex veinlet (arculus) between it and a clearly convex cubital vein, together with the absence of a developed convex vein MA corresponds to the 'paoliid line' pattern of wing venation of Kukalová-Peck and Brauckmann (1992, fig. 41). Such a convex arculus is also present in some taxa currently included in the Grylloblattodea, but they have a well developed convex MA, unlike this fossil. Those authors included the following families in the 'paoliid line': Paoliidae Handlirsch, 1906, Eucaenidae Handlirsch, 1906, Strephocladidae Martynov, 1938, Blattinopsidae Bolton, 1925, Synomaloptilidae Martynov, 1938, and Cymbopsidae Kukalová, 1965. Among these families, the Eucaenidae, Blattinopsidae, Strephocladidae, and Cymbopsidae strongly differ from *Mertovia* in their RP with numerous posterior branches. Carpenter (1992) included the Synomaloptilidae in the order Caloneurodea Handlirsch, 1937 but Béthoux *et al.* (2004) excluded them from this order. Rasnitsyn (Rasnitsyn & Quicke 2002) transferred them to the superorder Hypoperlidea Martynov, 1928. The medio-cubital pattern of *Synomaloptila* Martynov, 1938 remains poorly known but it differs from *Mertovia* in its cubital vein (CuA?) with only two distal branches (Carpenter 1992, fig. 128.1; Rasnitsyn & Quicke 2002, fig. 121).

Kukalová-Peck and Brauckmann (1992) added *Limburgina* Laurentiaux, 1950, but Béthoux and Nel (2002) noted that it is impossible to attribute it to the 'paoliid line' or to the Archeorthoptera Béthoux & Nel, 2002. The radial area of *Mertovia* is completely different from that of *Limburgina*. Kukalová-Peck and Brauckmann (1992) also included *Heterologopsis* in the 'paoliid line' but Béthoux and Nel (2002) demonstrated that it is an Archeorthoptera.

Rasnitsyn (Rasnitsyn & Quicke 2002) considered the Paoliidae to be the most inclusive group of the Pterygota, and as a unique family of the order Paoliida. Thus he did not follow the hypothesis of Kukalová-Peck and Brauckmann (1992) and considered the 'arculus' *sensu* Kukalová-Peck and Brauckmann (1992) as a very short vein M5. He also indicated that the Paoliida have no synapomorphies, which makes the characterisation of this order particularly difficult. Therefore, the phylogenetic relationships of the Paoliidae remain controversial and unresolved. Nevertheless, the wing venation of *Mertovia* is very similar to those of some Paoliidae like *Zdenekia* or *Paolia*, at least in the organisation of the cubito-median veins and the long RP with few apical branches.

Rasnitsyn (Rasnitsyn & Quicke 2002) included eight genera in the Paoliidae. *Zdenekia* shares with *Mertovia* a ScP separated from RA, but it is distinctly shorter, not reaching the wing apex, and unlike *Mertovia* its RP has three distal posterior branches (Kukalová 1958, text-fig. 1). The ScP of *Holasicia*, *Pseudofouquea*, *Paoliola*, *Olinka*, and *Paolia* ends in RA and the RP has numerous posterior branches (Melander 1903; Kukalová 1958, text-figs 3, 5, 9–12; Maples 1989, 1991). *Kemperala* also has a ScP ending in RA, but the RP in its fore wing is apparently simple and vanishes in the area between RA and M (Brauckmann 1984; Brauckmann *et al.* 1985).

Unlike *Mertovia*, *Sustaia* has a ScP ending in RA, but even if its RP is poorly preserved, it has no posterior branches in nearly all its length, as in *Mertovia* (Kukalová 1958, text-fig. 6, pl. 2, fig. 1). Another difference is the presence of numerous small branches of the anal vein in *Sustaia*, which is not apparent in *Mertovia*.

Carpenter (1992) considered the genus *Paolekia* Riek, 1976, originally included in the Paoliidae, as a 'Protorthoptera of family uncertain'. The difference between *Paolekia* and *Mertovia* lies in the wing apex, the RP of *Paolekia* having no fewer than four main branches (Riek 1976).

Handlirsch (1911) described the monotypic family Schuchertiellidae on the basis of a very incomplete wing base. Carpenter (1992) considered *Schuchertiella* Handlirsch, 1911 as *incertae sedis*. It has a strong oblique veinlet between a (probable) median vein and a (probable) cubital vein, but nothing is known about the convexity of these veins. Thus, it is not possible to determine if the family Schuchertiellidae belongs to the 'paoliid line' or to the Archaeorthoptera. Nevertheless, it differs from *Mertovia* in its basally forked alleged median and cubital veins.

Family ?Paoliidae Handlirsch, 1906

Genus undetermined

Figs 4, 5

Description: Distal two-thirds of wing uniformly dark, with clearly visible reticulate venation (so-called 'archaedictyon') and rather thick membrane, rather narrow elongate; fragment 31.1 mm long, estimated wing length about 50 mm, maximum width based on fragment 14.5 mm; only apex of concave vein ScP preserved, ending in convex RA, 26.1 mm from wing apex; several veinlets between RA(+ScP) and costal margin; simple RA reaching wing margin 5.5 mm above apex; numerous sigmoidal cross-veins between RA and RP; concave RP divided into two main branches 30 mm from wing apex, anterior branch subdivided into four branches and posterior one into three branches; no convex vein MA; concave vein interpreted as MP divided into two main branches, anterior one divided into three long branches and posterior one divided into two branches; apical parts of other veins CuA, CuP and probably anal veins visible.

Material examined: specimen B13190, part and counterpart of the apical part of a well preserved wing, uniformly dark (originally Šusta coll.). CZECH REPUBLIC: Upper Silesian Coal Basin, František Mine in Horní Suchá, hanging wall seam D (second etage); Upper Carboniferous, Westphalian A (Langsettian), Upper Suchá Beds (Member), Karviná Formation.

Discussion: Because of the absence of the structures of the basal half of the wing, its determination is tentative. Nevertheless, it has the main structures of the distal half of some paoliid wings, viz. apical fusion of ScP with RA, and absence of convex MA between concave RP and MP. This fossil differs from the wing of *Paoliola gurleyi* (Melander, 1903) only in the longer fusion of RA with ScP and longer distal branches of RP (Kukalová 1958). Therefore, we provisionally place it close to the Paoliidae.

Family **Katerinkidae** fam. n.

Type genus: *Katerinka* gen. n.

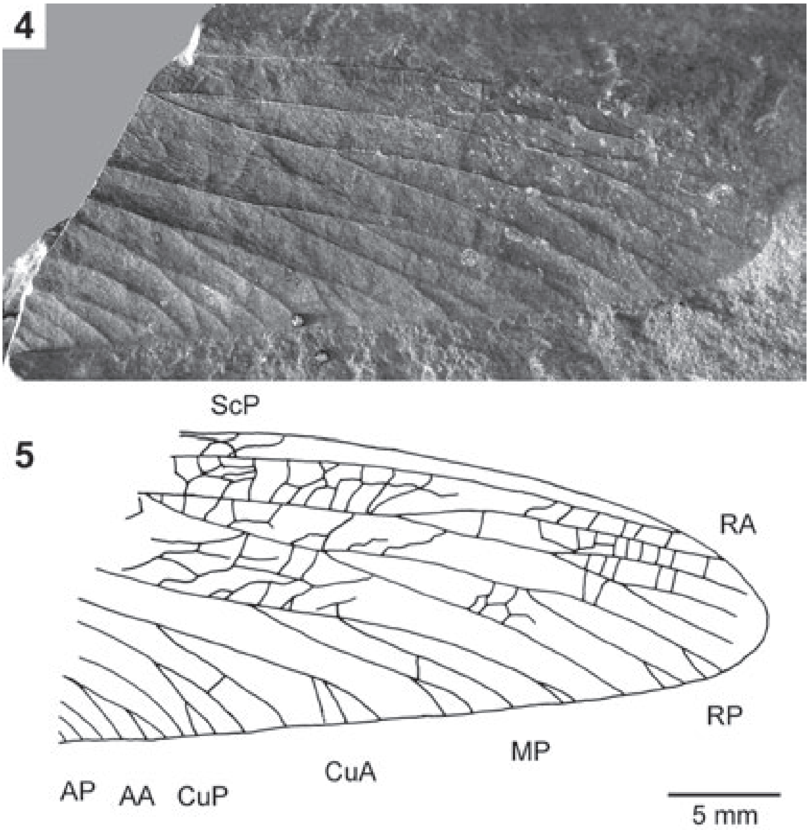
Diagnosis: Wide costal area between RA (+ScP) and C; vein ScP short, ending in RA slightly distad of RP base, in basal half of wing; RA with some anterior branches close to its apex; basal fork of RA/RP; concave RP with few distal branches; concave MP with two main branches rather basal to base of RP; rather pronounced convex 'arculus' between MP and convex CuA, basal to RP origin; area between CuA and CuP with net of veinlets; CuA with five distal posterior branches.

Genus **Katerinka** gen. n.

Etymology: Named after diminutive of Katerina (Katerinka in Czech), JP's daughter.

Type species: *Katerinka hilaris* sp. n., by present designation.

Diagnosis: As for the family.



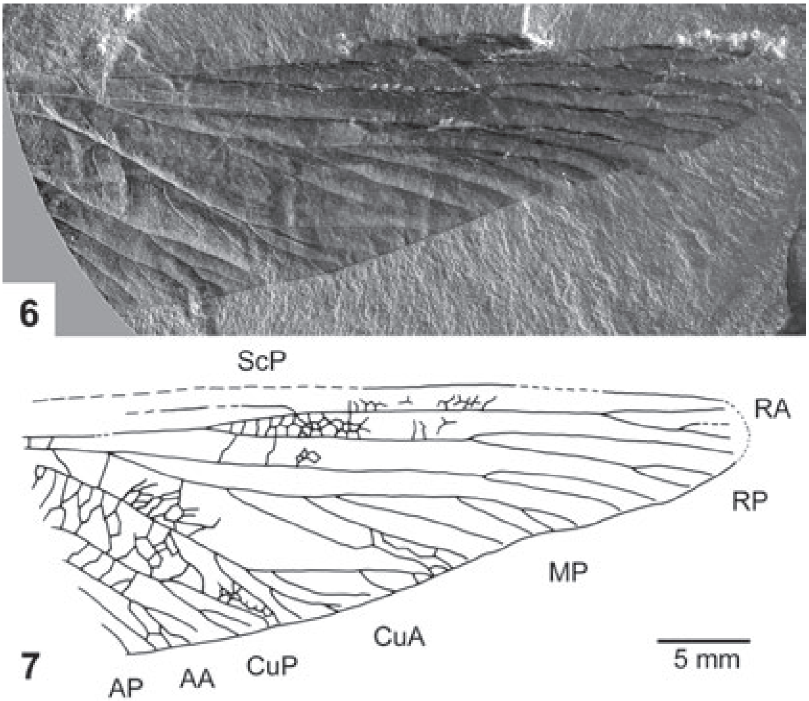
Figs 4, 5. Undetermined genus of presumed Paoliidae, photograph and line drawing of specimen B13190, collection of the Municipal Museum of Ostrava.

Katerinka hilaris sp. n.

Figs 6, 7

Etymology: From Latin *hilaris* (cheerful).

Description: Wing dark in coloration, with clearly visible reticulate venation (so-called "archaedictyon") and rather thick membrane, alternation of main veins not very prominent; wing fragment 40 mm long (estimated length about 50 mm), 15 mm wide (widest part at base of preserved portion); vein ScP rather poorly indicated as faint traces, but distinctly ending in RA only slightly distal of base of RP, very far from wing apex; net of small veinlets in area between C and RA (+ScP); RA convex, with three weak anterior branches near its apex; RA apparently ending near wing apex; RP base 30.2 mm from wing apex; RP concave with two main anterior branches, second terminally twigged; no convex vein MA, rather pronounced convex 'arculus' between concave median vein MP and convex CuA, 8.4 mm basad of RP base; MP divided into two main branches 5.5 mm basal to bifurcation RA and RP; anterior branch of MP straight, apically forked; posterior branch of MP with six posterior branches ending in posterior wing margin; distal part of CuA strongly sigmoidal, with five posterior branches



Figs 6, 7. *Katerinka hilaris* gen. et sp. n. (Katerinkidae fam. n.), photograph and line drawing of holotype specimen B11978, collection of the Municipal Museum of Ostrava.

ending in posterior wing margin but with no clear anterior branches; concave CuP with three apical branches; area between CuA and CuP with net of veinlets; two veins parallel to CuP, probably corresponding to anal veins, first apically forked.

Holotype: specimen B11978 counterpart of well preserved almost complete wing, missing basal part and tip of apex, costal area partly destroyed (originally Horák coll.). CZECH REPUBLIC: Upper Silesian Coal Basin, Doubrava Mine, borehole Cr 92, depth 201.8 m; Upper Carboniferous, Namurian–Westphalian A (Langsettian), absolute age about 315 Ma, Group of Hubert faunistic horizons, Lower–Upper Suchá Beds (Member), Karviná Formation.

Discussion: This fossil has the wing venation pattern of the 'paoliid line' sensu Kukalová-Peck and Brauckmann (1992), with a concave MP, no convex MA between MP and RP, a strong convex 'arculus' between convex CuA and MP, and a concave CuP. It differs from all the families that Kukalová-Peck and Brauckmann (1992) included in the 'paoliid line' in its short ScP ending in RA just distal to base of RP, and wide costal area between RA (+ScP) and C. Therefore we propose a new family for this fossil, probably closely related to the Paoliidae.

CONCLUSIONS

The new data support the hypothesis of favourable living conditions for paoliids within the territory of the Upper Silesian Coal Basin, since five of the eleven world species of paoliids are recorded from this locality (see check-list of Paoliidae in Appendix, Fig. 1). However, this bizarre phenomenon can be explained by insufficient records of

Late Namurian to Langsettian deposits elsewhere, and by a short period of existence of this group. Thus we prefer to retain both separate families, Paoliidae and Katerinkidae fam. n., without any strict relationship until the higher phylogeny of this group is resolved.

ACKNOWLEDGEMENTS

We kindly thank Eva Mertová (curator of palaeontology in the Municipal Museum in Ostrava) for her kind help and the loan of all specimens from the collection. We are grateful to Prof. Alex Rasnitsyn (Palaeontological Institute, Russian Academy of Sciences, Moscow) for suggestions and comments on the manuscript. The research was supported by a grant of the Ministry of Schools MSM 0021620828, partially by Grant Agency of the Czech Republic (No. 205/03/D151), and the Grant Agency of the Academy of Sciences (No. KJB301110701). This is a contribution to the project IGCP 469 (Late Westphalian terrestrial biotas and palaeoenvironments of the Variscan foreland and adjacent inframontane basins).

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Appendix

Updated check-list of described Paoliidae from Carpenter (1992):

Holasicia vetula Kukalová, 1958	Czech Republic (Upper Silesian Coal Basin)
Holasicia rasnitsyni Brauckmann, 1984	Germany (Hagen-Vorhalle)
Kemperala hagensis Brauckmann, 1984	Germany (Hagen-Vorhalle)
Mertovia sustai (Kukalová, 1958), **comb. n.**	Czech Republic (Upper Silesian Coal Basin)
Paolia vetusta Smith, 1871	USA (Indiana), The Netherlands (Limbourg)
Paoliola gurleyi (Melander, 1903)	USA (Indiana)
Pseudofouquea sp.	England (Bickershaw): Anderson *et al.* 1997
Pseudofouquea cambrensis (Allen, 1901)	Wales (Llanbradach Colliery)
Sustaia impar Kukalová, 1958	Czech Republic (Upper Silesian Coal Basin)
Zdenekia grandis Kukalová, 1958	Czech Republic (Upper Silesian Coal Basin)
Zdenekia occidentalis Laurentinaux, 1986	Belgium (Charbonnages de Ressaix)